The whole and the parts: relationships between floral architecture and floral organ shape, and their repercussions on the interpretation of fragmentary floral fossils

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THE WHOLE AND THE PARTS: RELATIONSHIPS BETWEEN FLORAL ARCHITECTURE AND FLORAL ORGAN SHAPE, AND THEIR REPERCUSSIONS ON THE INTERPRETATION OF FRAGMENTARY FLORAL FOSSILS[1]

Peter K. Endress[2]

ABSTRACT

Floral architecture and floral organ shape are interrelated to some extent as can be seen in the diversity of extant angiosperm groups. The shape of fragmentary fossil material, such as single organs, may therefore give hints for the reconstruction of the architecture of a flower. This study is partly a review and partly provides original material and new points of view on organ-architecture interrelationships. Several topics are illustrated with examples: (1) autonomous and imprinted shape, exemplified by cuneate organs, especially stamens; (2) conditions for valvate anther dehiscence; (3) lability in number and shape of reduced organs that have decreased in size and lost their original function; (4) long hairs as filling material of irregular spaces; (5) architectural conditions for the presence of orthotropous ovules; (6) structural differences between exposed and covered organ parts in bud; and (7) sepal aestivation and petal elaboration.

Key words: Autonomous shape, cuneate, floral architecture, imprinted shape, reduced organs.

There are relationships between the whole and the parts in floral structure. The ensemble of the floral organs constitutes the floral architecture, and, vice versa, the architecture of the whole flower or even inflorescence may have repercussions on the shape of individual organs. Under certain conditions, organ shape is conspicuously affected by the floral architecture. Thus, the shape of isolated organs may tell something about the architecture of flowers. Floral fossils are often not complete flowers, but are instead fragments and sometimes single organs. The question then arises on how the whole flower may have looked. Can certain traits of a flower be inferred from single organs, even if the systematic affinity is unknown? This is possible to some extent.

The influence of the floral architecture on the floral parts may be direct, shaped individually by neighboring organs during development. It may also be more indirect, shaped historically by evolutionary constraints on the best fit of the components of the floral architecture (Endress, 1975, 1994a). The first is seen in pressure marks on organs made by adjacent organs. The second is seen in harmoniously fitting parts within a (floral) bud. Both are related to economic use of space and protective function in the bud. In flowers at anthesis, the floral organs are also more or less highly synorganized with each other, which is related to the floral function in reproductive biology (Endress, 1994a, 2006).

The reconstruction and interpretation of floral fossils are important aspects in the integration of fossils into phylogenetic and evolutionary research. Information extracted from floral fossils is continuously being improved by technical advances in preparation and reconstruction (Schönenberger, 2005; De Vore et al., 2006; Friis et al., 2007; von Balthazar et al., 2007) and by the inclusion of fossils in morphological or combined molecular and morphological character matrices of extant plants for the determination of their phylogenetic position (Crepet & Nixon, 1998; Gandolfo et al., 1998; Sun et al., 2002; Friis et al., 2003a; Hermsen et al., 2003, 2006; Crepet et al., 2004). Conversely, information from extant flowers helps in the interpretation of related floral

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fossils (Crane et al., 1989; Friis & Endress, 1990; Endress & Friis, 1994, 2006; Doyle et al., 2003; Hermsen et al., 2003; Eklund et al., 2004).

This study tries to shed light on a neglected phenomenon that is informative in the understanding of floral architecture and organ shape, for paleobotanical reconstruction, and would also be of interest from a molecular developmental and evolutionary perspective. It is partly a review, but also presents original material.

Material and Methods

Species and specimens used for original illustrations are listed in Appendix 1.

Material used for light microscopy (LM) or scanning electron microscopy (SEM) was fixed in formalin/acetic acid/alcohol (FAA) or 70% ethanol. For serial microtome sections, specimens were either embedded in paraplast and the section series stained with safranin and Astra blue or embedded in Technovite (2-hydroethyl methacrylate; Hereus Kulzer, Wehrheim, Germany) and stained with ruthenium red and toluidine blue. Sections were mostly 5–10 μm thick. For SEM studies, specimens were treated with 2% osmium tetroxide, dehydrated in ethanol and acetone series, critical point–dried, and sputter-coated with gold.

Autonomous Shape and Imprinted Shape (Superimposed by Contiguous Neighbors)

The influence of mechanical pressure on the shape of plant organs has rarely been studied, perhaps in contrast to animals (Benjamin & Hillen, 2003), although the influence of mechanical stimulation on plants is conspicuous (Braam, 2005). It is useful to distinguish between autonomous and imprinted shape. Autonomous shape is the shape of an organ developing without physical influence from contiguous organs. Imprinted shape is the shape of an organ altered by the pressure of contiguous organs (Endress, 1975, 1994a, 2006). There are various intensities of this effect. In the extreme case (level 1), irregular imprints of adjacent contiguous organs are present on the affected organ. This goes so far that the disassembled organs can be put together like the pieces of a jigsaw puzzle (Fig. 1A, B). If two such organs are of the same kind (e.g., two stamens), the mutual effect is about equal in both. If they are of different kinds, one of them is more deformed than the other. As an example, in a floral bud of an Annonaceae, the deforming influence of the stamens on the carpels is more pronounced than that of the carpels on the stamens for most of their length. This is shown on transverse sections by broad indentations within carpel flanks but lesser indentations in stamen flanks (Fig. 1A, left side). In addition, the peripheral stamens of the bud are shaped by the three inner perianth organs; the peripheral line is relatively smooth and shows three corners at the site of the margins of the three inner perianth organs (Fig. 1B). Thus, in these two examples it appears that the outer (older) organs influence the inner (younger) organs more than the other way round. In a less extreme case (level 2), there is no or less direct local deformation, but the organs fit tightly together in a harmonious way. As an example, in a floral bud of *Gillbeea adenopetala* F. Muell. (Cunoniaceae), the stamens of the two whorls have filaments of different lengths, and thus the anthers are orderly stacked in two superposed rows (Fig. 2A). However, there are also cases in which, in contrast to an orderly stacking, the floral organs are not orderly stuffed in bud, e.g., in flowers with a high number of stamens; such flowers may then have somewhat distorted anthers in bud, but the shape may be more or less restored when the flowers are open and the pressure is released, e.g., *Barringtonia calyptrata* R. Br. ex Benth., Lecythidaceae (Fig. 2B, C) (Endress, 1994a).

In general, it appears that stamens or carpels affected by imprinted shapes are more common in basal angiosperms and basal eudicots than in core eudicots or monocots. However, there are exceptions of such stamens in core eudicots, especially in flowers in which the perianth and androecium are not highly synorganized and that have irregular numbers of perianth and androecium organs. An example is the elusive genus *Sphenostemon* Baill., which was once classified (as *Idenburgia* Gibbs) with Trimeniaceae (Austrobaileyales) (Perkins, 1925), one of the basalmost angiosperm families. In complete contrast, today *Sphenostemon* is in a family of its own (Sphenostemonaceae) of uncertain position in the euasterids II (Savolainen et al., 2000; APG, 2003). Its earlier erroneous placement was because of the general appearance of its flowers and in part because of its irregularly cuneate stamens without an anther that is clearly differentiated from the filament. The stamens are densely crowded in bud and have an imprinted shape by mutual pressure (Fig. 2D–G) (see also Endress, 2002).

However, the reverse may also occur: imprinted shapes may play a role in highly regular and synorganized flowers. In Asclepiadoideae (Apocynaceae), the two carpels fuse postgenitally in their uppermost part and this united region attains a pentangular shape, molded by the five adjacent anthers (e.g., Endress, 1990). Thus, the apex of the anthetic gynoecium looks like a pentamerous struc-

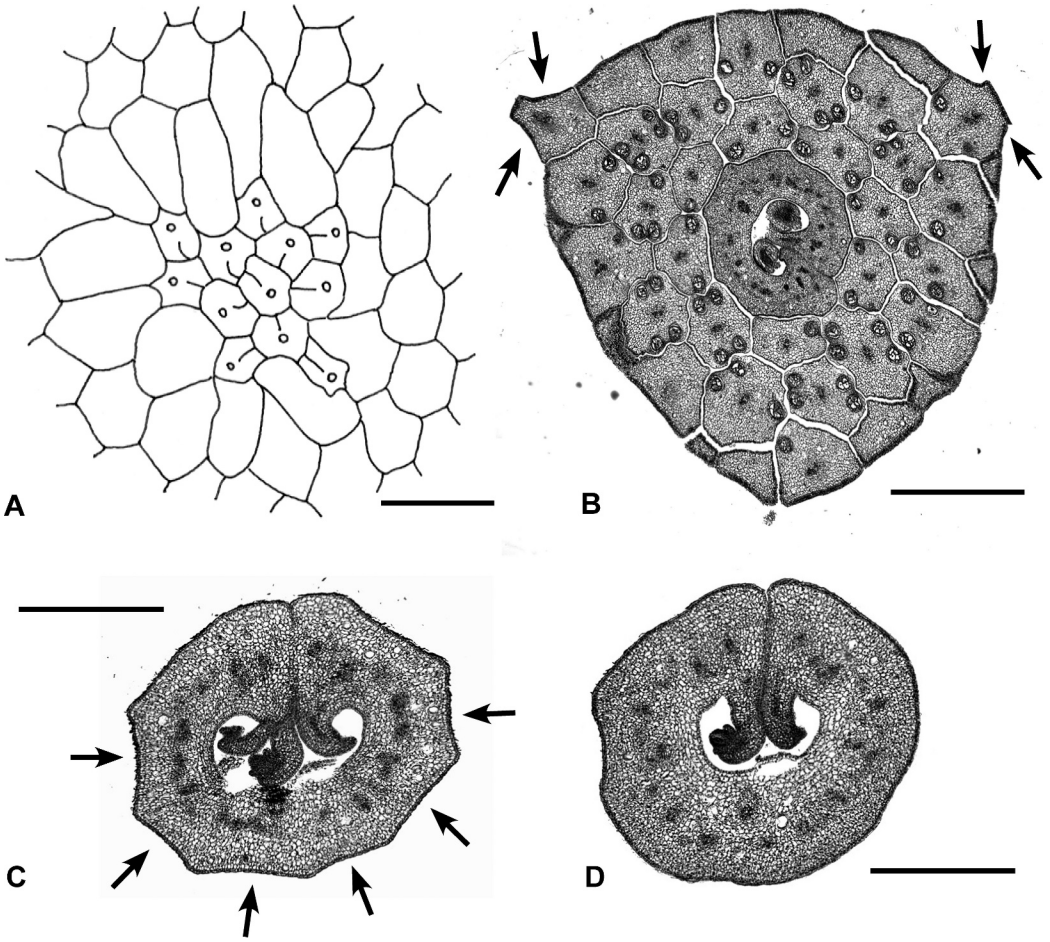

Figure 1. Autonomous and imprinted shape in flowers of Annonaceae. —A. *Cananga odorata* Hook. f. & Thomson, transverse section of floral center with inner stamens and carpels (with ventral slit and dorsal vascular bundle indicated). All organs are contiguous and arranged like the pieces of a jigsaw puzzle by mutually imprinted shapes. The section is slightly oblique (lower on the right side than on the left). On the left side, the stamens shape the carpels, and on the right side the carpels shape the stamens. B–D. *Cyathocalyx martabanicus* Hook. f. & Thomson, transverse sections. —B. Androecium and unicarpellate gynoecium. The stamens shape each other and the gynoecium, and the periphery of the androecium is shaped by the three inner (removed) tepals (arrows). —C. Gynoecium shaped by stamens (arrows). —D. Same gynoecium with autonomous shape at the base where the inner stamens are united into a ring and the imprinting influence of single stamens is lacking. Magnification bars: A, B = 1 mm; C, D = 0.5 mm.

ture, although it is dimerous. Mutual adjustment of adjacent organ surfaces is necessary for postgenital fusion of the five stamens with the upper part of the gynoecium in these highly synorganized flowers. The developmental processes involved in this adjustment are largely unknown (see also Endress, 2006).

However, such imprinted shapes are not commonly used for subsequent postgenital fusion. A similar quadrangular shape of a dimerous gynoecium, imprinted by four stamens, is present in *Triaenophora* Solereder (Plantaginaceae) (Wang & Wang, 2005). In some Lauraceae, the monomerous gynoecium attains a triangular shape in early development, molded by the trimerous preceding whorls. This has led to the erroneous interpretation of a trimerous nature of the lauraceous gynoecium (Singh & Singh, 1985), although monomery is evident from comparative developmental studies (Endress, 1972).

Shape of a floral primordium may also be influenced by adjacent parts of the inflorescence. Instead of being circular (*Couroupita* Aubl., Lecythidaceae; Fig. 3A), it can be transversely extended, especially if the inflorescence is elongate and the flowers have a reduced perianth (e.g., *Euptelea* Siebold & Zucc., Eupteleaceae, Fig. 3B, and Endress, 1986; Ren et al., 2007; *Styloceras* Kunth ex A. Juss., Buxaceae, von Balthazar & Endress, 2002). It can also be asymmetrical, if the inflorescence is monochasial

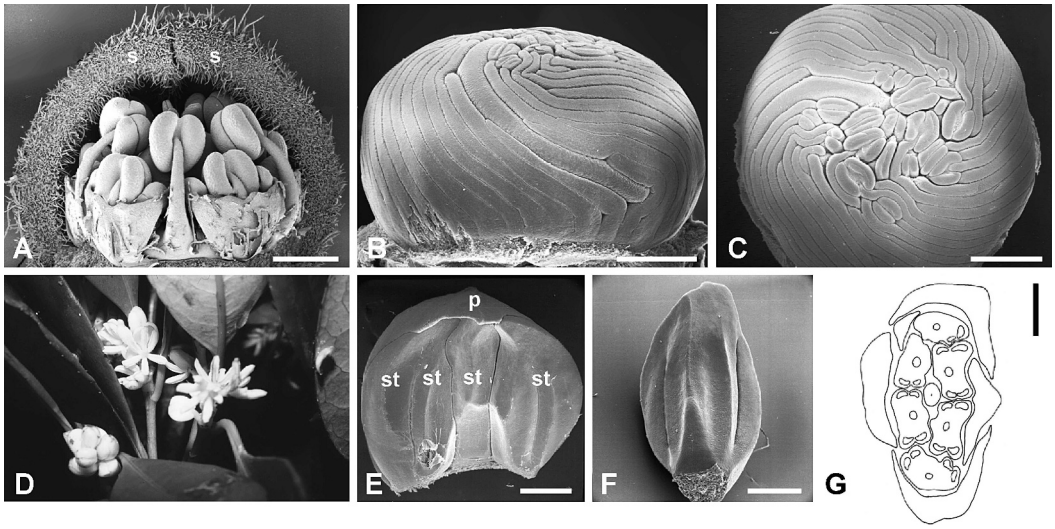

Figure 2. Spacing in buds. —A. *Gillbeea adenopetala* F. Muell. (Cunoniaceae). Regular spacing of the two whorls of five stamens within the floral bud, covered by five valvate sepals (s). B, C. *Barringtonia calyptrata* (Lecythidaceae), androecium, perianth removed. Irregular spacing (stuffing) of the numerous stamens in bud, anthers with imprinted shape by mutual deformation. —B. Bud view from the side. —C. Bud view from above. D–G. *Sphenostemon lobosporus* (F. Muell.) L. S. Sm. (Sphenostemonaceae). —D. Flowering shoot. —E. Perianth part (p) and four stamens (st) from bud, irregularly contiguous. —F. Stamen from bud (from ventral), showing irregular, imprinted shape. —G. Transverse section of bud with tight arrangement and imprinted shape of anthers. Magnification bars: A = 0.5 mm; B, C = 1 mm; E–G = 0.2 mm.

(e.g., Heliconiaceae, Strelitziaceae, Kirchoff, 2003). The difference in shape of floral primordia may be especially striking if inflorescences have both a lateral and a terminal flower, such as in *Drimys* J. R. Forst. & G. Forst. (Winteraceae), in which the different shape of the floral primordium has repercussions on floral phyllotaxis of lateral versus terminal flowers (Doust, 2001). Not only can floral primordia be asymmetric but inflorescence primordia can be as well, if they are under space constraints or under the influence of a polarity induced by the entire plant or a larger unit of the plant, such as in Loteae (Leguminosae) with a superposed dorsiventrality (Sokoloff et al., 2007). In *Euptelea* (see above), in addition to the

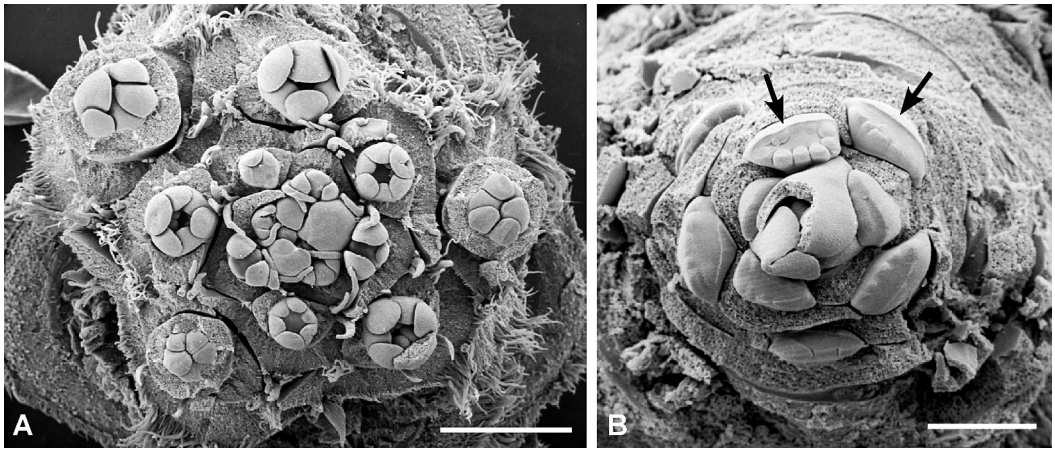

Figure 3. Shape of floral primordia. A–B. Young inflorescence tips from above. —A. *Couroupita guianensis* Aubl. (Lecythidaceae), floral primordia and young flowers widely spaced, round, with autonomous shape. —B. *Euptelea polyandra* Siebold & Zucc. (Eupteleaceae), floral primordia and young flowers crowded, flattened, with imprinted shape; the abaxial transverse line is caused by pressure of the subtending bract (arrows). Magnification bars: A = 1 mm; B = 0.5 mm.

general transversely extended shape, direct pressure by the subtending bract leaves its mark on the abaxial side of the young flower (Fig. 3B).

Architectural Conditions for the Presence of Cuneate or Shield-shaped Organs

An example for imprinted shape are Lower Cretaceous isolated fossil stamens, many of which show two striking features: (1) cuneate (wedge-shaped) anthers and a massive apex, and (2) anther dehiscence by laterally hinged valves and not by simple longitudinal slits (Friis et al., 1991, 2006a). Such cuneate stamens (anthers) also occur in some extant plants (Figs. 4, 5) (Endress, 1975; Endress & Hufford, 1989; Hufford & Endress, 1989). We may ask: Are cuneate stamens typical for certain clades, or is this shape due to certain architectural constraints independent of systematic relationship? Both questions can be answered affirmatively to some extent. The first aspect, cuneate shape, which is related to imprinted shape, will be addressed in this section; the second aspect, valvate dehiscence, will be addressed in the next section.

Isolated cuneate (wedge-shaped) anthers with a massive sterile apex and short filament indicate with some probability that the anthers were contiguous and densely arranged in bud, that the anther apex had a protective function and was not covered in bud by other organs, and that stamen arrangement was in a spherical, hemispherical, or cylindrical fashion. Therefore, the surface of the entire architecture is largest at the periphery, which results in the cuneate form of the stamens. There are two possibilities for such an architecture: (1) inflorescences with dense flower arrangement and the perianth lacking or small and not protective, such as in extant *Hedyosmum* Sw. (basal angiosperms) (Fig. 4A–C), Platanaceae (basal eudicots) (Fig. 4D–F), Altingiaceae (basal core eudicots) (Fig. 4G–I), Sparganiaceae (Fig. 4J–L), and Typhaceae (Fig. 4M–O) (both commelinid monocots), and (2) single flowers with numerous stamens, such as in Annonaceae (Fig. 5) and *Nuphar* Sm. in Nymphaeaceae, both basal angiosperms (Endress, 1975, 1987). In Platanaceae, the female inflorescences have a similar architecture as the male ones, and the carpels have a cuneate ovary (Crane, 1989). In some Annonaceae (although they have a well-developed protective perianth), the stamens become exposed in late bud, and thus their broad apices are then the protective parts for the thecae and the ovaries. In both cases, the massive anther apices may also be a protection against pollinators with biting mouth parts or other herbivorous insects. Thus, for isolated fossil stamens with such a shape, even if they may not be determined as to their larger alliance (if pollen is lacking), partial reconstruction of the architecture of their flowers or inflorescences may be possible.

Cuneate carpels arranged in a spherical gynoecium occur in *Kadsura marmorata* (Hend. & Andr. Hend.) A. C. Sm. in Schisandraceae (Smith, 1947), and cuneate gynoecia (without perianths and subtending bracts) arranged in a spherical inflorescence occur in *Pandanus* S. Parkinson (pers. obs.).

There are not only cuneate floral organs but also other kinds of cuneate organs with a protective function and similar dense arrangement into cone-like architectures. In extant plants, bracts that subtend flowers or partial inflorescences (cymes) are often cuneate or have a shield-like portion at the periphery of the bud of dense inflorescences (e.g., Piperaceae [Fig. 6A–C], Mimosoideae of Leguminosae [Fig. 6D–F], and Betulaceae [Fig. 6G–I], Endress, 1975; Balanophoraceae, Kuijt, 1969; Moraceae, Berg, 1990). This is also true for sporangiophores of various gymnosperms and groups other than seed plants (e.g., *Equisetum* L. [Fig. 6P–R], Endress, 1975; Taxaceae [Fig. 6M–O], Endress, 1975; Mundry & Mundry, 2001; cycads [Fig. 6J–L], Endress, 1975; Mundry & Stützel, 2003). Cuneate organs are also known from a number of various fossil plants. Subtending bracts (or sporangiophores) are cuneate in some lycophytes (*Mazocarpon* Benson; Schopf, 1941; Pigg, 1983), sphenophytes (*Palaeostachya* Weiss; Baxter, 1955), cycads (*Androstrobus* Schimper, *Beania* Carruthers, Harris, 1941, 1964; *Delemaya* Klavins, Taylor, Krings & Taylor, Klavins et al., 2003), and many conifers (Ohsawa, 1994; Stockey, 1994). Ovules are cuneate in Pentoxylales (Sahni, 1948; Crane, 1985) and interseminal scales in Bennettitales (Harris, 1969; Crepet, 1974; Sharma, 1982; Pedersen et al., 1989; Nishida, 1994; Rothwell & Stockey, 2002; Stockey & Rothwell, 2003). The formation of such massive peripheral, contiguous protective parts is commonly provided not by a small-celled, cytoplasm-rich marginal meristem but mainly by cell enlargement (Endress, 1975). The well-preserved Bennettitales described by Crepet and Delevoryas (1972) also indicate that cell enlargement alone was instrumental in the thickening of the peripheral, protective part of the ovular integument in female reproductive structures.

Conditions for Valvate and Simple Longitudinal Dehiscence in Anthers

The second striking feature of fossil Lower Cretaceous stamens (Friis et al., 2006a: fig. 21), in addition to the cuneate shape (see above), is that a number of them have a valvate dehiscence pattern with two laterally hinged valves in each of the two

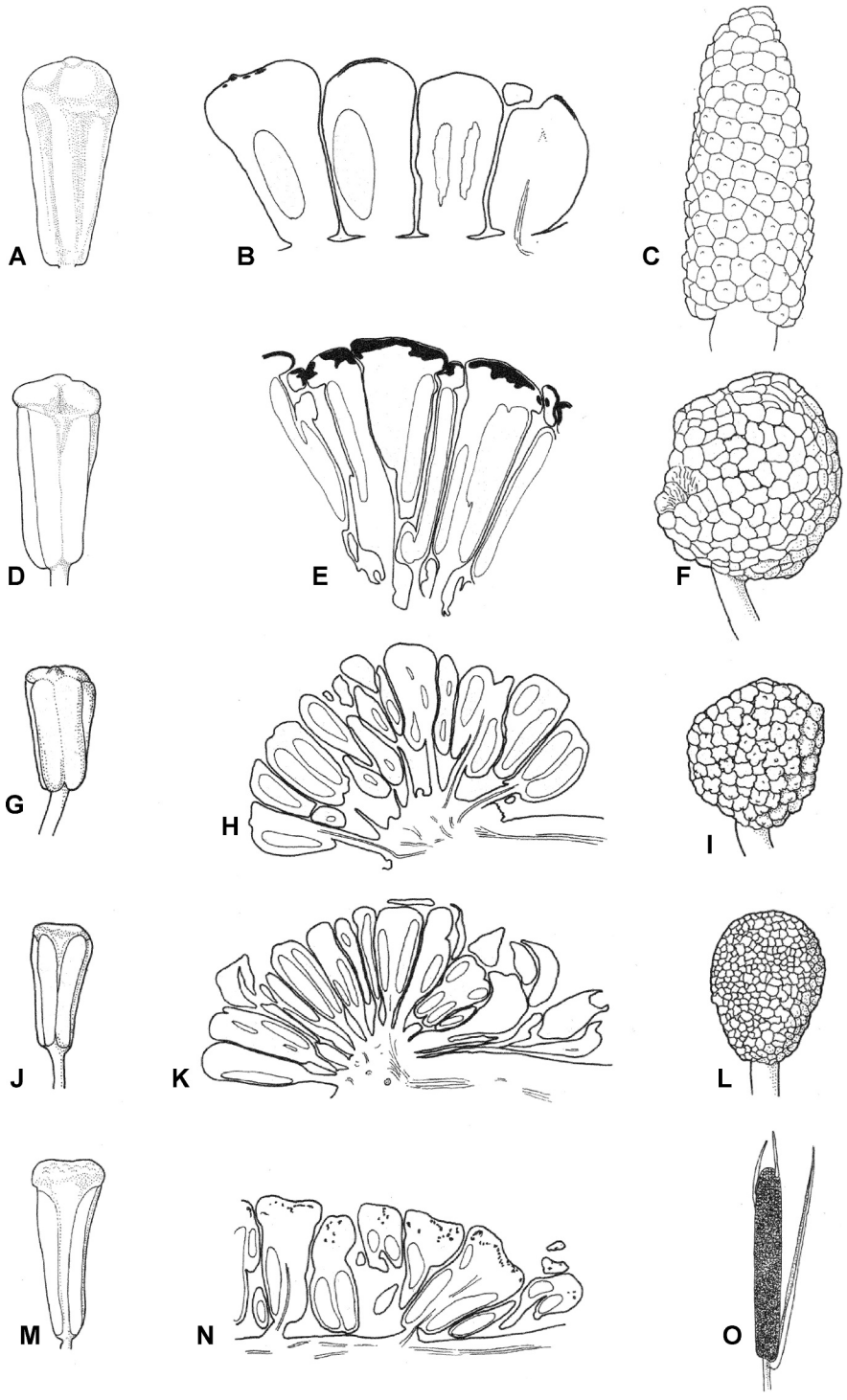

Figure 4. Cuneate anthers and spherical or cylindrical young inflorescences bearing flowers with reduced perianth. —A, D, G, J, M. Stamen (anther). —B, E, H, K, N. Longitudinal section of part of the inflorescence showing contiguous stamens. —C, F, I, L, O. Entire inflorescence. A–C. *Hedyosmum mexicanum* C. Cordem. (Chloranthaceae). D–F. *Platanus orientalis* L. (Platanaceae). G–I. *Liquidambar styraciflua* L. (Altingiaceae). J–L. *Sparganium erectum* L. (Sparganiaceae). M–O. *Typha minima* Funck in Hoppe (Typhaceae). Tanniferous tissue black in B, E, N. (From Endress, 1975, with permission; <http://www.schweizerbart.de>).

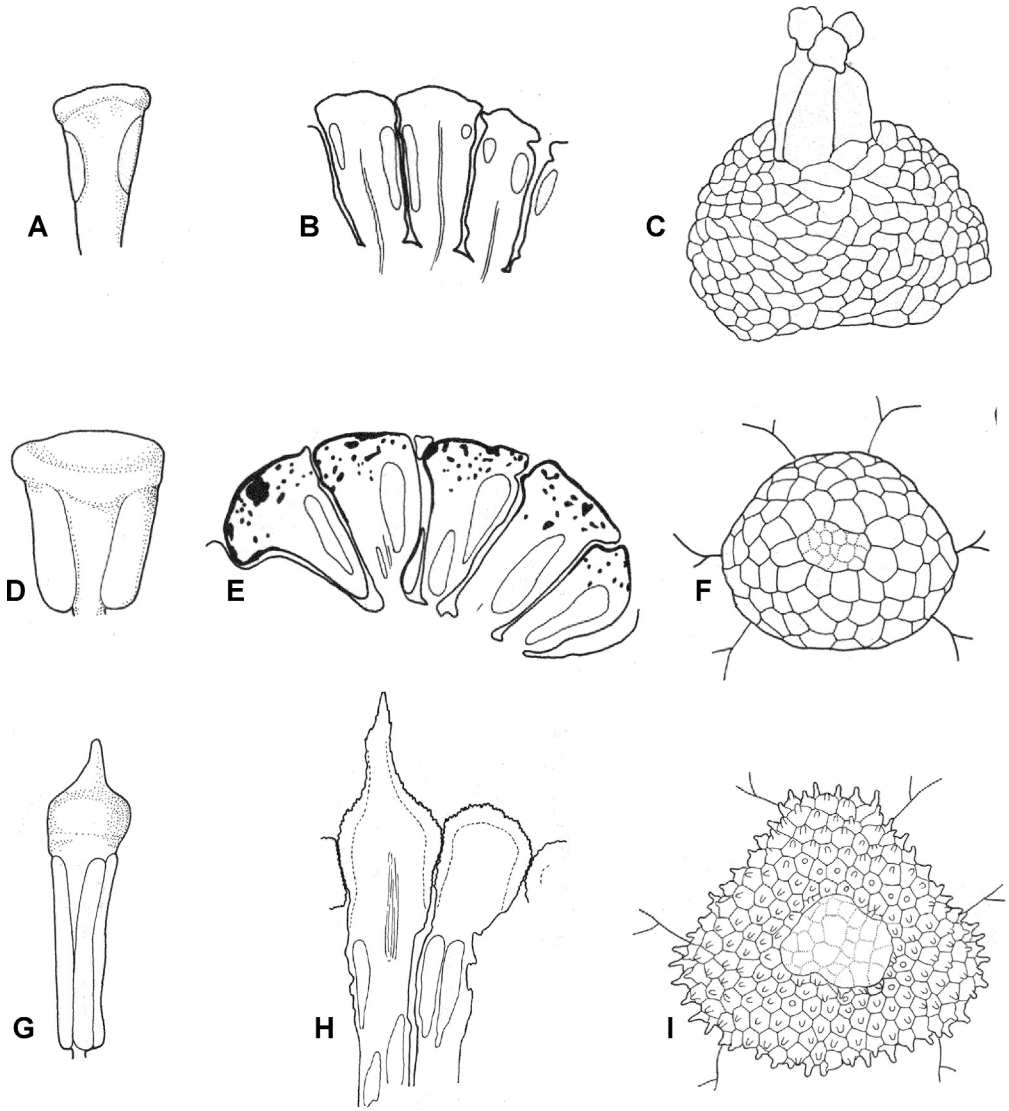

Figure 5. Cuneate anthers and hemispherical androecia in Annonaceae. —A, D, G. Stamen (anther). —B, E, H. Longitudinal section of part of the androecium showing contiguous stamens. —C, F, I. Androecium and gynoecium. A–C. *Asimina triloba* (L.) Dunal. D–F. *Polyalthia longifolia* (Sonn.) Thwaites. G–I. *Cananga odorata* (Lam.) Hook. f. & Thomson. Tanniferous tissue black in E. (From Endress, 1975, with permission; <http://www.schweizerbart.de>).

thecae, which open in the manner of saloon doors; this is also true for extant taxa with a similar anther shape. A variant of laterally hinged valves are apically hinged valves, which do not act in pairs that open together but open each pollen sac separately (restricted to some Laurales). Anthers with a thin connective (and therefore bulging pollen sacs) can easily be deformed after dehiscence (Fig. 7A–C), which allows efficient opening, and for such opening it is sufficient to have simple longitudinal dehiscence. Anthers with a thick connective, however, cannot be deformed so easily because of architectural constraints, and, therefore, valvate dehiscence is more efficient (Fig. 7D–F).

Valvate stamens with this architecture (thick connective) are concentrated in some clades and not common in angiosperms as a whole. Although these clades are in disparate places in the angiosperm tree, they are more or less restricted to basal angiosperms and basal eudicots. Such anthers were recorded among basalmost angiosperms in Nymphaeales (*Nuphar*; Hufford, 1996); among other basal angiosperms in Laurales (*Sinocalycanthus* (Cheng & S. Y. Chang) Cheng & S. Y. Chang and some fossil Calycanthaceae;

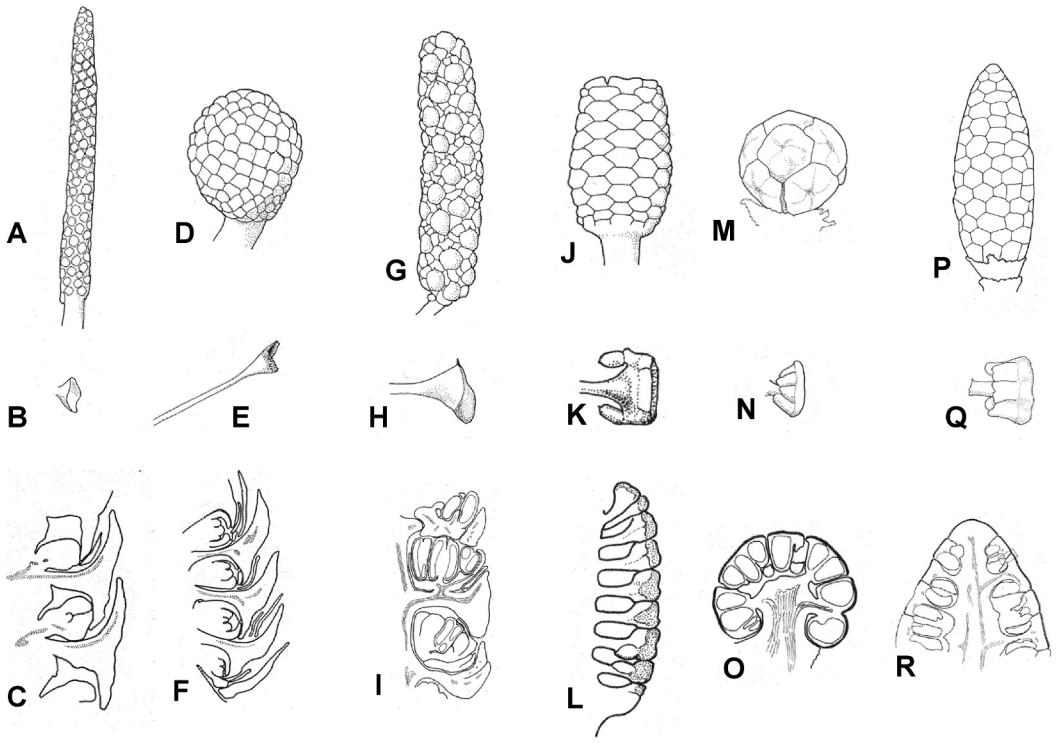

Figure 6. Cuneate subtending bracts of flowers or partial inflorescences or sporangiophores, and hemispherical or cylindrical inflorescences or shoots with sporangiophores. —A, D, G, J, M, P. Inflorescences or shoots with sporangiophores. —B, E, H. Subtending bracts. —K, N, Q. Sporangiophores. —C, F, I, L, O, R. Longitudinal sections of (parts of) A, D, G, J, M, and P. A, B. *Peperomia rotundifolia* (L.) Kunth (Piperaceae). C. *P. caperata* Yunck. (Piperaceae). D–F. *Leucaena latisiliqua* (L.) Gillis & Stearn (Leguminosae). G–I. *Alnus glutinosa* (L.) Gaertn. (Betulaceae). J–L. *Zamia verschaffeltii* Miq., female (Zamiaceae). M–O. *Taxus baccata* L. (Taxaceae). P–R. *Equisetum arvense* L. (Equisetaceae). (From Endress, 1975, with permission; <http://www.schweizerbart.de>).

Friis et al., 1994; Crepet et al., 2005; Staedler et al., 2007; Atherospermataceae, Lauraceae, Hernandiaceae, Monimioideae–Monimiaceae; Endress & Hufford, 1989), Magnoliales (Annonaceae [Fig. 8A], Magnoliaceae, Eupomatiaceae, Himantandraceae, Degeneriaceae; Endress & Hufford, 1989), and Piperales (*Piper augustum* Rudge; Endress, 1994b); among basal eudicots in Ranunculales (Eupteleaceae; Endress, 1986; Ranunculaceae p.p.; Endress & Hufford, 1989; Weber, 1993), Proteales (Platanaceae [Fig. 8B]; Hufford & Endress, 1989), and Trochodendraceae (Endress, 1986; Hufford & Endress, 1989; Chen et al., 2007); and among basal core eudicots in Saxifragales (Altingiaceae, Hamamelidaceae [Fig. 8C]; Endress, 1989; Hufford & Endress, 1989). Valvate anthers appear to be absent from monocots and higher core eudicots.

Lability in Number and Shape of Reduced Organs That Have Decreased in Size and Lost Their Original Function

Reduced organs that have decreased in size (i.e., have become shorter and narrower) and lost their original function may become labile in number and shape because functional constraints on shape are lacking. A reduction in size and loss of function of an organ type may be concomitant with a decrease in number, but the reverse—an irregular increase in number—is also possible. What are the conditions for maintaining a constant number of organs in whorls?

In eudicots, sepals are basically the protective organs in floral buds. They are commonly quincuncial-imbricate (with overlapping flanks) or, less often, valvate (with margins of adjacent sepals tightly appressed to each other). Especially in the latter case, all sepals of a flower have the same shape and their number is stable, as they have to build a precise envelope for the young floral organs (e.g., *Heisteria* Jacq., Olacaceae) (Fig. 9A). However, here and there in the phylogenetic tree, the protective function has been evolutionarily transferred from the sepals to another organ category (e.g., petals) or, less often, floral subtending bracts or prophylls. If petals have become protective, they commonly become larger than the sepals early in development and often have a valvate aestivation in bud. The sepals have then

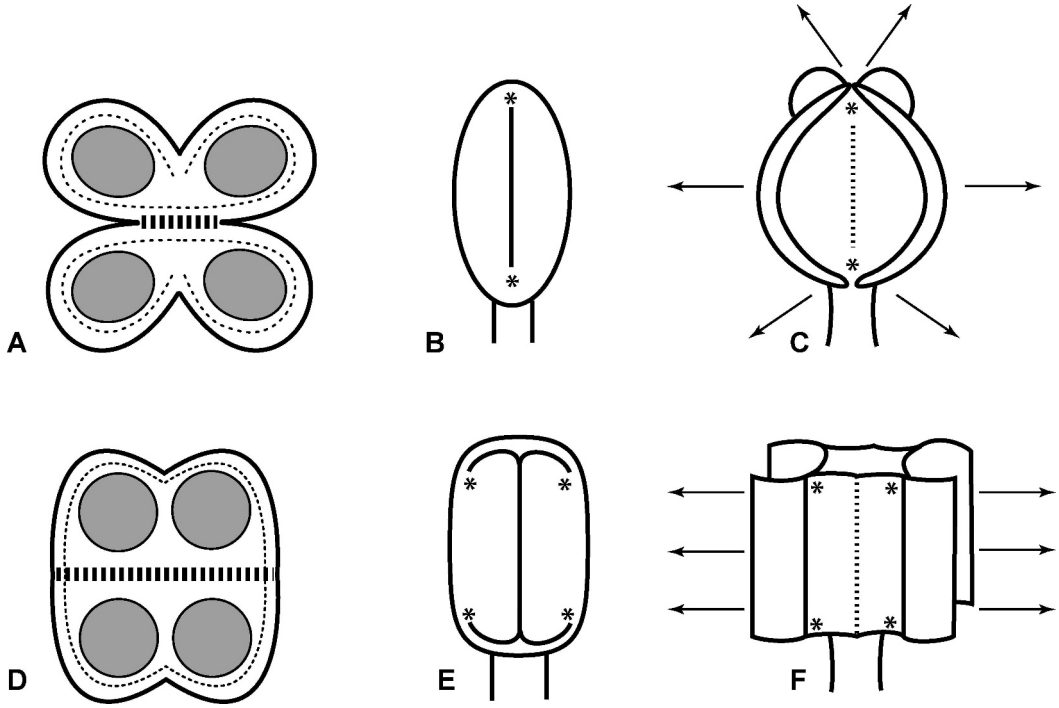

Figure 7. Anthers with opening by longitudinal slits (A–C) and laterally hinged valves (D–F). —A, D. Transverse section of anther before dehiscence (thick, interrupted line indicates thickness of anther; thin, interrupted lines indicate endothecium; gray areas indicate pollen sacs). —B, E. Anther before dehiscence, from transverse side, showing theca with dehiscence lines (asterisks indicate ends of dehiscence lines). —C, F. Anther after dehiscence, from transversal side (interrupted line indicates septum between the two pollen sacs of a theca; asterisks indicate ends of dehiscence lines; arrows indicate directions of opening of theca).

commonly become small and sometimes irregular in shape and number. In some cases, the number has irregularly increased. This irregularity is due to a lack of a functional constraint on a precise number and shape of the organs. An example is *Mimosa* L. (Leguminosae), in which several subgroups have a valvate corolla (Fig. 9C) and a highly reduced calyx, which is irregularly denticulate, with more teeth than

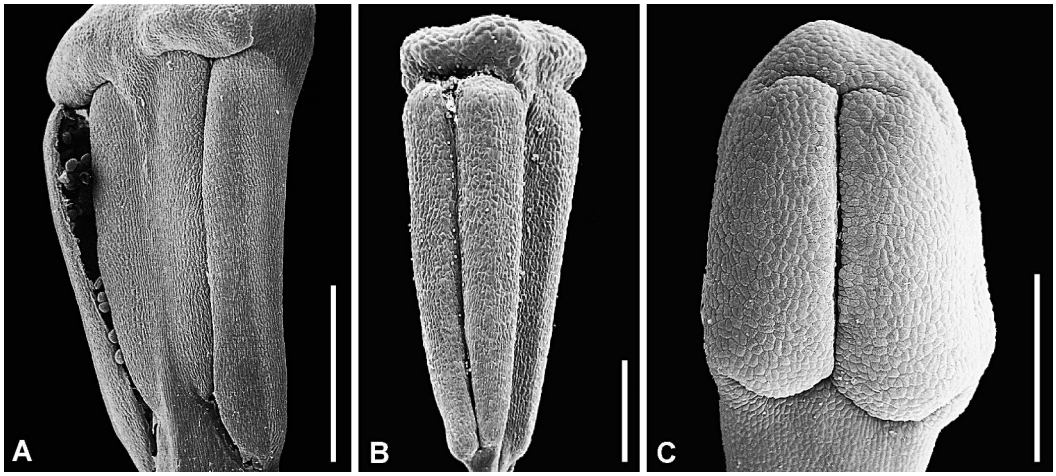

Figure 8. Anthers with dehiscence by two laterally hinged valves for each theca. —A. *Artabotrys hexapetalus* (L. f.) Bhandari (Annonaceae). —B. *Platanus orientalis* L. (Platanaceae). —C. *Fothergilla major* Lodd. (Hamamelidaceae). Magnification bars: A–C = 0.5 mm.

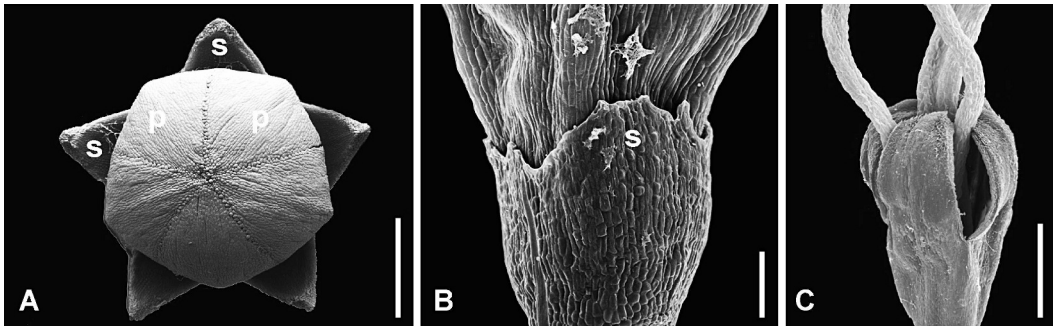

Figure 9. Well-developed versus reduced perianth organs. —A. *Heisteria parvifolia* Sm. (Olacaceae), sepals and petals well developed, both with valvate aestivation. B, C. *Mimosa spegazzinii* Pirotta (Leguminosae). —B. Sepals reduced, with open aestivation. —C. Petals well developed, with valvate aestivation. p = petals, s = sepals. Magnification bars: A, C = 0.5 mm; B = 0.1 mm.

would be expected from the merism of the flower (Fig. 9B) (see also Tucker, 1984; Barneby, 1991). Even more conspicuous examples are Asteraceae and Valerianaceae, in which the originally pentamerous calyx is dissolved into more than five pappus bristles (e.g., Semple, 2006).

Thunbergia Retz. and related genera (Thunbergioideae, Acanthaceae) (Schönenberger & Endress, 1998; Schönenberger, 1999) are examples for bracts as protective floral organs. As in most Lamiales, the basic sepal number in Acanthaceae is five, and the sepals are protective in bud. However, in Thunbergioideae, the mechanical protective function for the flowers has been transferred to two large prophylls, which are postgenitally united in bud (Fig. 10A). In contrast, the sepals are not protective at any stage of floral development (except indirectly for bearing extranuptial nectaries, which attract ants that defend the flowers against herbivores) (Fig. 10B). Thus, the sepals are much reduced in size and sometimes completely lost. However, if present, they often have irregularly increased in number from originally five to 15 or more in some species; they form short scales of slightly variable size. In sphingid-pollinated species (e.g., *T. guerkeana* Lindau) with increased flower length, these ca. 15 narrow organs may be secondarily elongate in terms of evolution (Fig. 10C) (Schönenberger, 1999).

Subtending bracts are another possibility for surrogate protective organs if the sepals are reduced. In Balanophoraceae, which has massive protective bracts, male flowers of *Helosis* Rich. still have

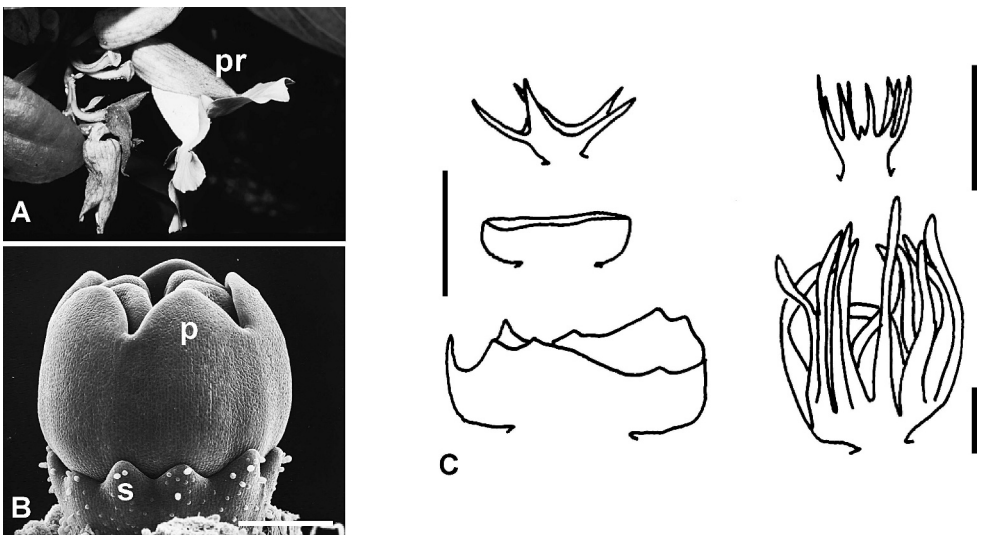

Figure 10. *Thunbergia*, reduced calyx. —A. *T. grandiflora* Roxb., open flower from the side. —B. *T. alata* Sims, young flower bud. —C. Calyx differentiation in five species of *Thunbergia*. p = petal, pr = prophyll, s = sepal. Magnification bar: B = 0.25 mm; C = 5 mm.

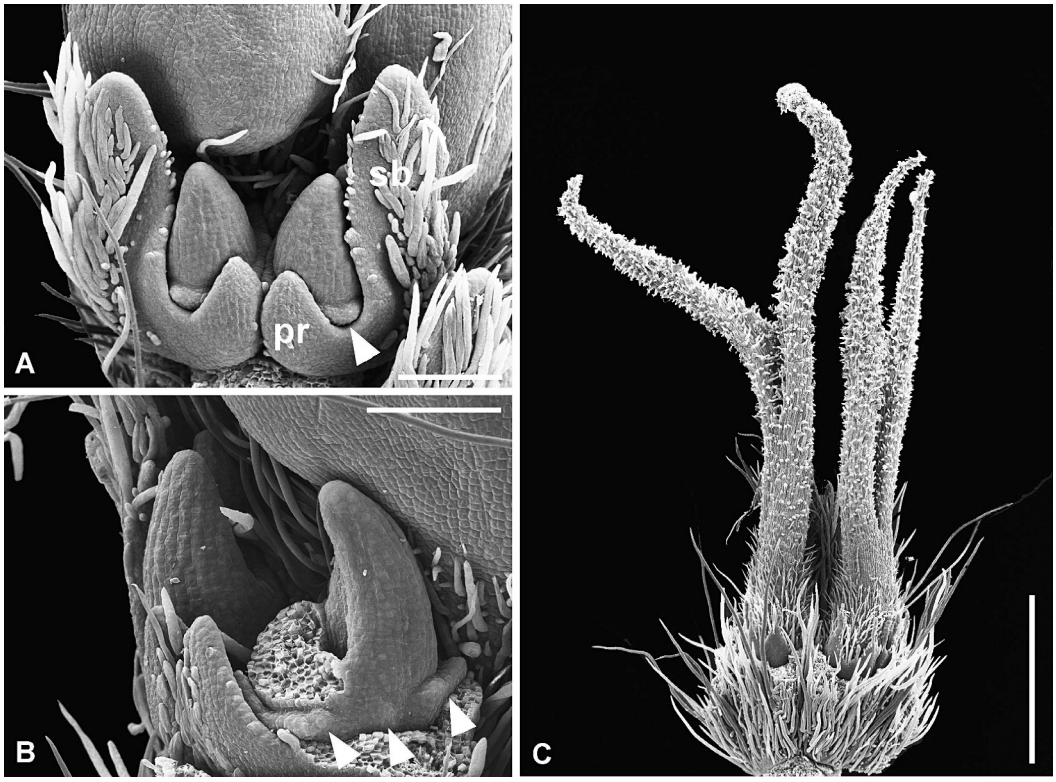

Figure 11. *Carpinus betulus* (Betulaceae), female flowers, with reduced calyx. —A, B. Two flower buds in a dichasium at sepal initiation; in B, one of the carpels of one of the two flowers removed. —C. Two flowers in a dichasium, at anthesis. pr = prophyll, sb = subtending bract, arrowheads = sepal primordia. Magnification bars: A, B = 0.2 mm; C = 1 mm.

protective, valvate sepals of a fixed number, whereas those of the closely related *Corynaea* Hook. f. have nonprotective, reduced sepals with irregular shape and increased, unstable number (Kuijt, 1969). *Parrotia* C. A. Mey. and *Sycopsis* Oliv. (Hamamelidaceae) also have reduced, nonprotective sepals with irregular shape and increased, unstable number, in contrast to other Hamamelidaceae with larger, protective sepals with a fixed number and shape (Endress, 1989, 1990).

A last example, female flowers of *Carpinus* L. (Betulaceae), should be treated in more detail. In contrast to the male flowers of *Alnus* Mill. and *Betula* L. with four and two protective sepals, according to tetramerous and dimerous flowers, respectively, in *Carpinus* (Abbe, 1935), the sepals are not protective; they are short, of irregular shape, and increased in number. However, although in *C. betulus* L. sepal number and shape are irregular (Eichler, 1878), there are commonly four somewhat larger sepals in the median and transverse planes, which is still reminiscent of a basic tetramerous pattern (Abbe, 1935; Endress, 1967). Protective organs for the young flowers are the subtending bract of each flower pair, which represents a dichasium without a central flower, plus the subtending bract and the two prophylls of each single flower (Fig. 11C). The sepals are much delayed in development, and at no time do they enclose the inner parts of the flower. Sepal delay is so pronounced that they only appear after the two carpels have been initiated. They first appear as two irregular rims, each in the median plane of the bicarpellate gynoecium (Fig. 11A, B). Each sepal (or calyx tooth) ends in a colleter in early development—a secretory tip that probably has a chemical, and not mechanical, protective function for the young flower (Figs. 12, 13). Later in development, pronounced longitudinal ribs develop in the calyx teeth extending along the surface of the inferior ovary and are most conspicuous in fruit (Fig. 13). In these ribs, strong vascular bundles are situated, which probably differentiate so strongly due to the early secretory function of the colleters, which they serve. Such pronounced ribs are also present in fossil Betulaceae-like flowers (Schönenberger et al., 2001; Friis et al., 2003b, 2006b).

In *Carpinus betulus*, structural lability is expressed at the level of the individual (Fig. 12A–H) and between individuals (Fig. 13A–F). Within an individ-

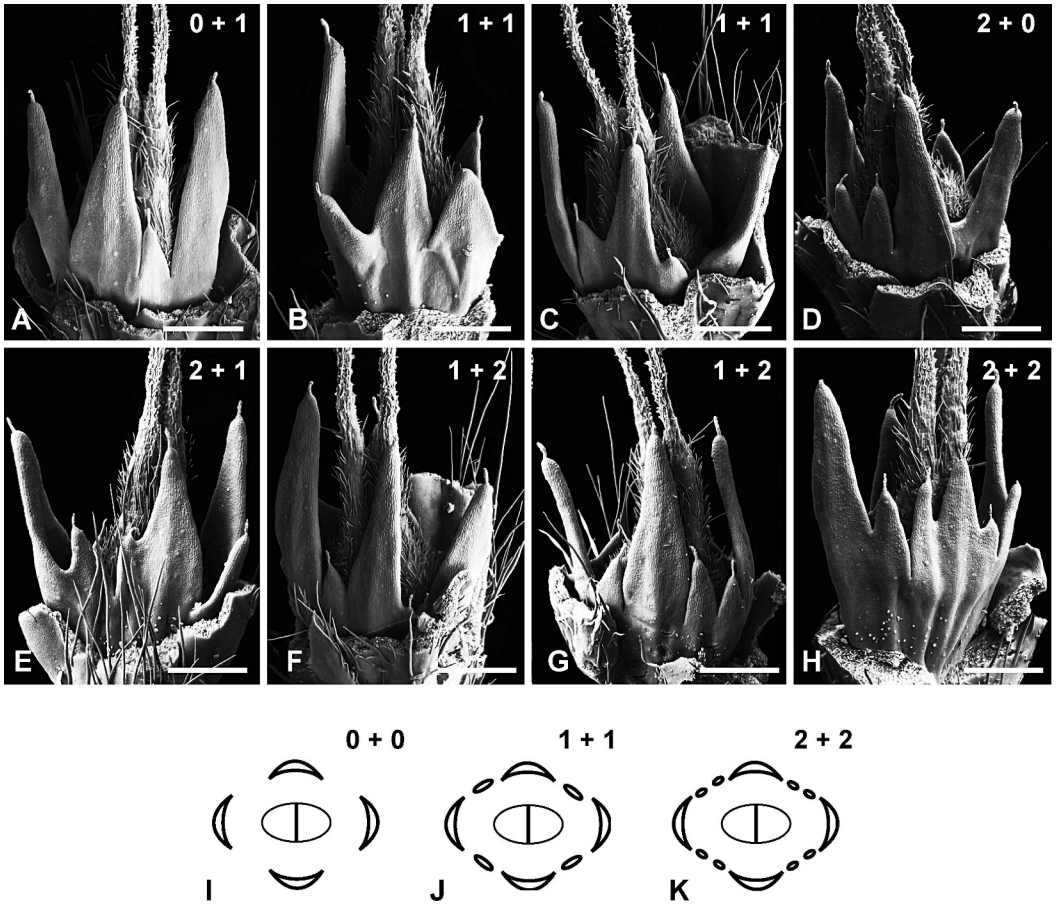

Figure 12. *Carpinus betulus* (Betulaceae). —A–H. Female flowers from a single tree showing intra-individual variability of sepal formation, with corresponding sepal formula of the visible side indicated at upper right. —I–K. Floral diagrams with corresponding sepal formula of one side of the flower indicated. Magnification bars: A–H = 0.5 mm.

ual, between the commonly four larger sepals in the median and transverse planes there may be zero, one, or two commonly smaller sepals. Within a flower, all these numbers may be present without a recognizable pattern (Fig. 12A–K). Inter-individual variation can be seen by comparing developmental series of flowers from two different trees (Fig. 13A–F). In the second tree, the sepals are shorter, more numerous, and, in older stages, more curved so that in the fruit they form a more convoluted rim (Fig. 13F) than in the first tree (Fig. 13C).

Thus, in both *Thunbergia* (Acanthaceae) and *Carpinus* (Betulaceae), the sepals appear to have convergently lost their mechanical protective function with size reduction and concomitant loss of a fixed size, shape, and number, but perhaps secondarily gained a secretory protective function. Therefore, small sepals of irregular size associated with secretory structures in fossil flowers may indicate that they did not have a mechanical protective function and that their number may be variable.

Increase in number concomitant with reduction in size and loss of function is not only present in sepals. It may also occur in stamens. An example is the large genus *Bauhinia* L. (Leguminosae), in which the basic number of 10 stamens in two whorls as common in the family may be reduced to five, three, or even a single stamen. In *B. galpinii* N. E. Br., only the three lower (anterior) stamens of the outer androecial whorl are well developed (Fig. 14A, D). The other seven stamens are variously reduced to small staminodes without anthers (Fig. 14C, D) (Endress, 1994a). The two upper staminodes of the outer whorl are still larger than those of the inner whorl. In the inner whorl, the organs are increased in number. In the expected position of each single organ, there are two or three tiny collateral organs (Fig. 14B, D). In *Dillenia* L. (Dilleniaceae), the flowers have numerous stamens

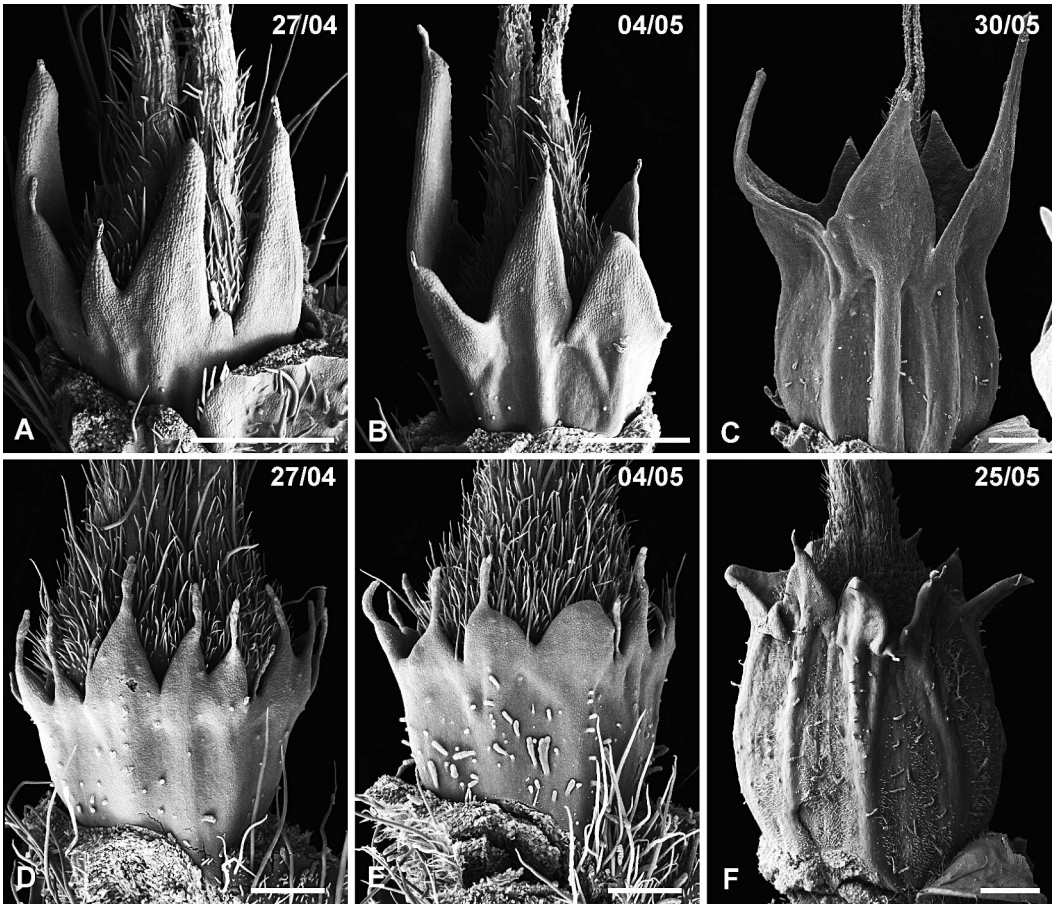

Figure 13. *Carpinus betulus* (Betulaceae). A–F. Female flowers from two different trees, in the same developmental stages (dates of collection indicated), showing inter-individual variability of sepal formation. —A–C. Same tree as Figure 12A–H. —D–F. Another tree. Magnification bars: A–C, F = 0.5 mm; D, E = 0.25 mm.

that are centrifugally initiated. The last initiated organs of the androecium are staminodes. They are narrower than the stamens, and two collateral organs occupy a position in which a single organ would be expected (Endress, 1997: fig. 8B).

Long Hairs as Filling Material of (Irregular) Spaces

The presence of long hairs concentrated in certain areas of flowers is sometimes an indication of irregular spaces in flower buds, as hairs may be used as flexible filling material, which may have protective functions against herbivores or physical factors (e.g., drought or frost). Such hairs occur preferably at or around carpel bases. There they may also play a role in fruit development. Examples are seen in Hamamelidaceae and Cunoniaceae (Matthews & Endress, 2002), which have only two carpels but have five, 10, or more stamens. In these flowers, long hairs are at and around the ovary (Fig. 15A–D). In some Monimiaceae, the carpels are free in the bottom of a floral cup, and hairs develop in the interspaces between the carpels (Fig. 15E) (Endress, 1980). In *Munroidendron* Sherff (Araliaceae), the hairs are filling material for the open space in the floral center that originates by an increased number of carpels in a whorl (Fig. 15F) (Endress, 2006). In Moraceae, protective hairs between floral organs or flowers are also common (Berg, 1990).

Another instance is hairs on anthers, as seen in male flowers of *Carpinus* (and other Coryleae, Betulaceae). Here, sepals are not only reduced as in female flowers but completely absent. The inner space of the bud is provided by the subtending floral bract and the bracts of the adjacent flowers, and has an irregular shape so that the anthers cannot be tightly packed in a strict pattern. Thus, the space is not spherical, as often in flowers, but broad and flat. To fill this space, these flowers have two unusual features: (1) the two thecae of each anther are

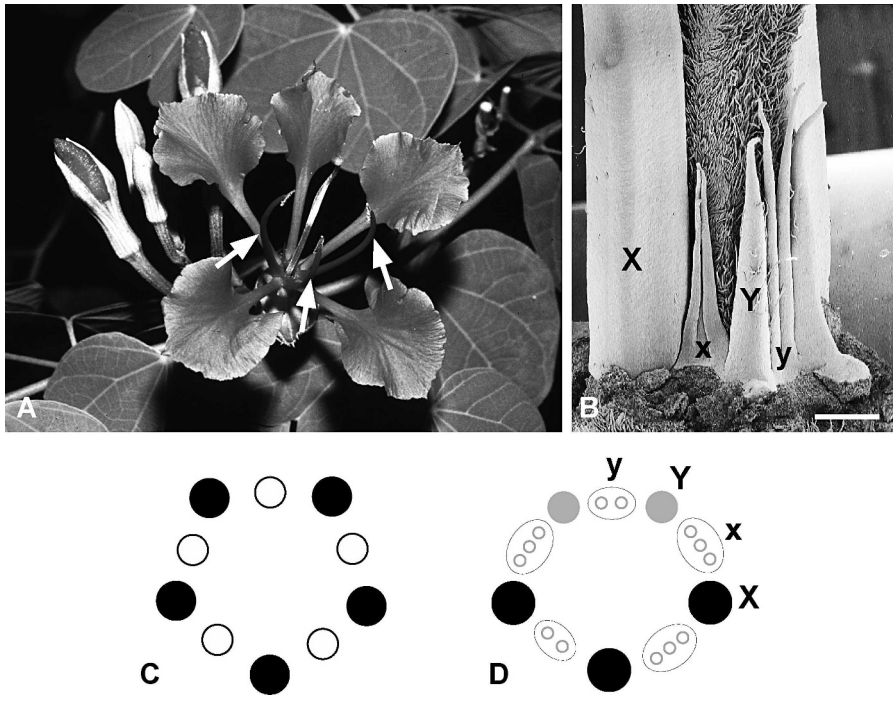

Figure 14. *Bauhinia galpinii* N. E. Br. (Leguminosae), reduction of androecium and concomitant increase in number of reduced organs. —A. Flower with three fertile stamens (arrows). —B. Stamen and staminode of outer whorl (X, Y) and staminodes increased in number of inner whorl (x, y). —C. Diagram of androecium common in many Leguminosae (black: organs of outer whorl, white: organs of inner whorl). —D. Diagram of androecium of *Bauhinia galpinii*, showing increase in number of strongly reduced staminodes of inner whorl (black and gray: organs of outer whorl; white: organs of inner whorl; letters corresponding to those in Fig. 14B). Magnification bar: B = 0.5 mm.

separated from each other by a filamentous connective, which allows flexible arrangement of the thecae (Fig. 15H); and (2) again, long hairs fill empty spaces. These hairs occur as tufts on top of each theca (Fig. 15G, H). Such hairs on anthers are present in a few unrelated groups of wind-pollinated plants with a reduced perianth (e.g., some Anacardiaceae, Fagaceae, Juglandaceae) (Elias, 1972; Endress & Stumpf, 1991; Bachelier & Endress, 2007). It would also be interesting to know whether the presence of hairs on these anthers is just a consequence of sepal reduction and a concomitant irregular space in bud, or whether it has acquired an additional ecological function in the context of pollen dispersal by wind.

Architectural Conditions for the Presence of Orthotropous Ovules in Angiosperms

In contrast to other seed plants, angiosperms commonly have anatropous ovules. Ovules with this shape have the micropyle topographically adjacent to the placenta and, thus, can take up pollen tubes directly from the placenta. Nevertheless, orthotropous ovules occur sporadically or regularly in some larger groups. They conspicuously tend to occur under certain conditions of the ovary architecture, three of which are listed here. Commonly, the inner architecture of the ovary is such that the pathway of pollen tubes from the stylar canal to the micropyle of the ovules is alleviated by the orthotropous shape.

(1) The most simple condition is the presence of a single basal (or almost basal) ovule, which positions its micropyle directly to the lower end of the stylar canal, thus enabling direct passage of a pollen tube (Fig. 16A, D, G). This condition has evolved in many different angiosperm families, such as in Piperaceae (basal angiosperms; Igersheim & Endress, 1998), Didymelaceae (basal eudicots; von Balthazar et al., 2003), Polygonaceae p.p. (core eudicots, Caryophyllales), Juglandaceae and Myricaceae (core eudicots, rosids, Fagales), Urticaceae (core eudicots, rosids, Rosales; Eckardt, 1937), Zosteraceae (basal monocots; Dahlgren, 1939), and Araceae (basal monocots).

(2) If the locule is filled with secretion, ovules of any number can be orthotropous as the pollen tubes may directly grow through the secretion (e.g., Buzgo, 1994) (Fig. 16B, E, H). This condition is known from a number of plants that grow in wet or moist habitats,

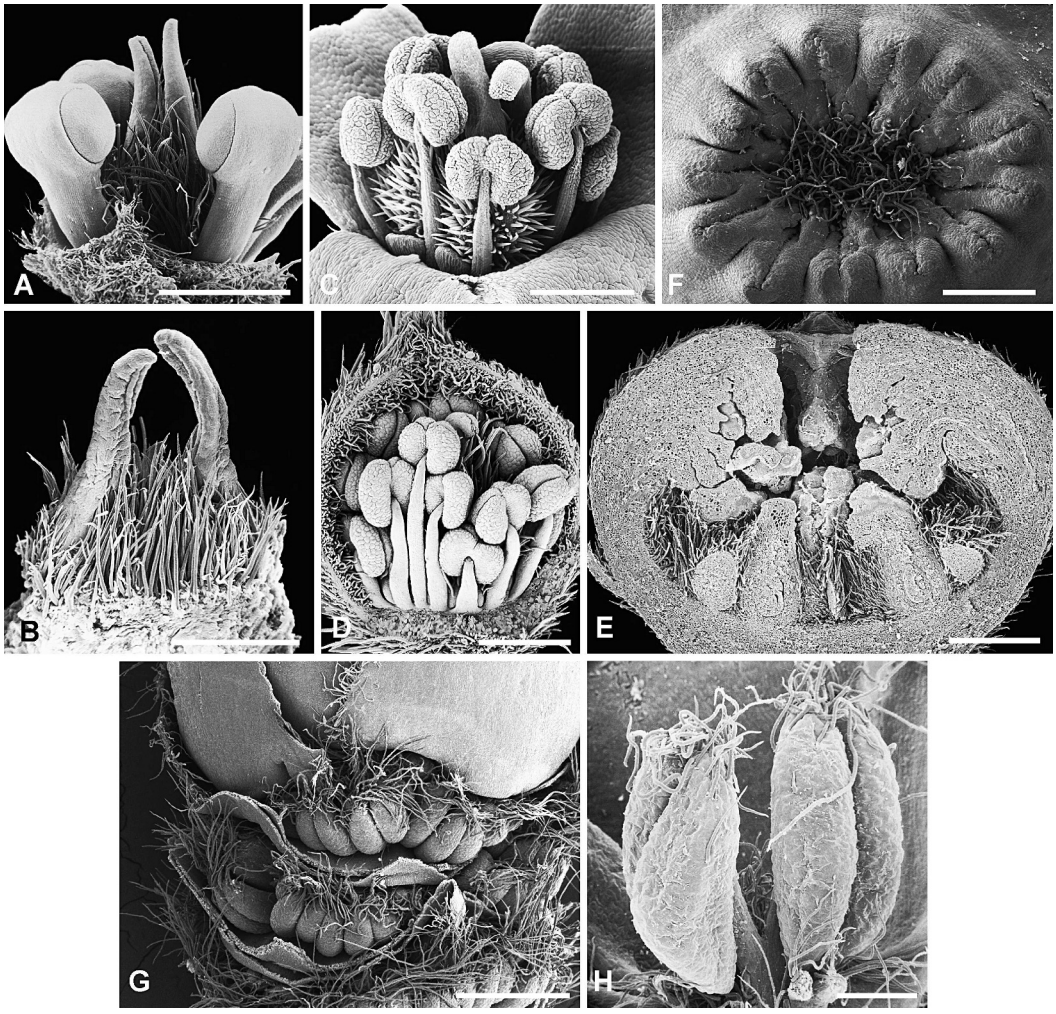

Figure 15. Long hairs as filling material of empty spaces in floral buds and flowers. —A. *Hamamelis virginiana* L. (Hamamelidaceae). —B. *Trichocladus grandiflorus* Oliv. (Hamamelidaceae). —C. *Acsmithia davidsonii* (F. Muell.) Hoogland (Cunoniaceae). —D. *Geissois biagiana* F. Muell. (Cunoniaceae). —E. *Wilkiea* sp. indet. (Monimiaceae). —F. *Munroidendron racemosum* (C. N. Forbes) Sherff (Araliaceae). G, H. *Carpinus betulus*, male (Betulaceae). —G. Part of male inflorescence, flower-subtending bracts partly removed. —H. Stamen, with the two thecae flexible by filamentous connective and crowned by tuft of long hairs. Magnification bars: A, B, F = 0.5 mm; C = 0.3 mm; D = 0.4 mm; E, G = 1 mm; H = 2 mm.

such as in *Barclaya* Wall. of Nymphaeaceae (basalmost angiosperms; Schneider, 1978; Igersheim & Endress, 1998), Acoraceae (basal monocots; Rudall & Furness, 1997; Buzgo & Endress, 2000; Igersheim et al., 2001), *Pistia* L. and other Araceae (basal monocots; Buzgo, 1994), and some Hydrocharitaceae (basal monocots; Igersheim et al., 2001).

(3) If the placentae are parietal, the micropyle of orthotropous ovules may be directed not to their own placenta but to the neighboring placenta, where they take up pollen tubes (Fig. 16C, F, I). Examples are *Casearia* Jacq. (core eudicots, rosids, Malpighiales) and Mayacaceae (monocots, commelinids).

These three architectural conditions for the presence of orthotropous ovules were briefly discussed in Endress (1994a). There are also other instances of orthotropous ovules, in which the ovary architecture does not so evidently favor the orthotropous condition as in the three types mentioned.

Structural Differences Between Exposed and Covered Organ Parts in Bud

Organ surfaces that are exposed in bud may behave differently from those that are covered in bud. This is especially conspicuous in imbricate aestivation,

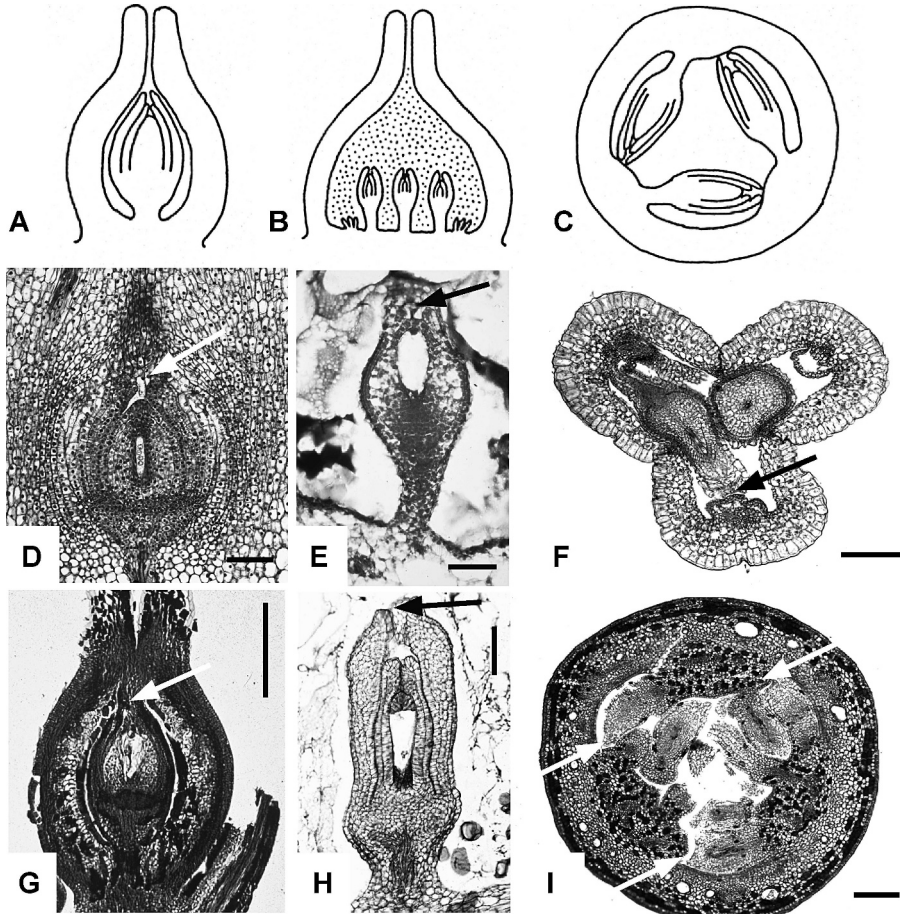

Figure 16. Orthotropous ovules and ovary architecture in angiosperms. —A, D, G. A single ovule at the base of a locule, with micropyle directed to stylar canal. —B, E, H. Several ovules in a spacious locule filled with secretion. —C, F, I. Several ovules in a locule with parietal placentae, with micropyles directed to neighboring placenta. A–C. Schematic figures of ovaries with ovules. D–I. Microtome sections of ovaries with ovules. —D. *Piper augustum* (Piperaceae). —E. *Hydrocharis morsus-ranae* L. (Hydrocharitaceae). —F. *Mayaca* sp. indet. (Mayacaceae). —G. *Polygonum filiforme* Thunb. (Polygonaceae). —H. *Pistia stratiotes* L. (Araceae). —I. *Casearia silvana* Schltr. (Salicaceae) (arrows point to micropyle). Magnification bars: D, E, H = 0.1 mm; F, I = 0.2 mm; G = 0.5 mm. (A, B, C from Endress, 1994a. Reprinted with permission from Cambridge University Press.)

where the same organ has exposed and covered areas. For instance, if there is an indument of hairs, the hairs may be restricted to or more strongly developed on the exposed areas (*Stellaria media* (L.) Vill., Nelson, 1954; *Chiranthodendron* Larreat., *Fremontodendron* Coville, von Balthazar et al., 2006; *Rivea* Choisy, Staples, 2007; *Convolvulus tricolor* L., pers. obs.). Another difference is that the exposed flanks are green whereas the covered flanks are hyaline (*Ipomoea purpurea* (L.) Roth., pers. obs.). The most detailed study on this positional effect is that by Warner et al. (2005, in press) for *Nuphar* and other Nymphaeaceae.

Often in imbricate aestivation the margins are thin (two cell layers). The thin part of the covered flanks is often broader than that of the exposed flanks within a flower (e.g., sepals in Caryophyllaceae, Rohweder, 1970; *Corynocarpus* J. R. Forst. & G. Forst., Matthews & Endress, 2004; *Brexia* Noronha ex Thouars; petals in *Siphonodon* Griffith, Matthews & Endress, 2005a; and sepals and petals in *Ixerba* A. Cunn., Matthews & Endress, 2005b). This influence of the position on the differentiation of the sepal flank is especially obvious in pentamerous flowers with quincuncial aestivation. The third-formed sepal of the five has a covered and an exposed flank, and the covered flank is regularly thinner than the exposed flank (Rohweder, 1970). A well-known example are the sepals of rose flowers, in which the exposed margins have pinna-like appendages, whereas the covered margins lack them; Troll

(1957) cites a rhyming Latin riddle on this behavior of rose sepals, which reportedly goes back to Albertus Magnus (13th century).

In valvate tepal, sepal, or petal aestivation, the organs have thick, abruptly ending margins, they are triangular, and the curvature of the margins reflects the shape of the bud—the more curved the margins are, the shorter and rounder the bud. Among floral fossils, the monocot *Mabelia* Gandolfo, Nixon & Crepet has such valvate tepals (Gandolfo et al., 2002).

Sepal Aestivation and Pinnate Petals

Petals that are elaborate and have several lobes along the margins (pinnate shape) tend to occur in flowers with valvate calyx aestivation (Endress & Matthews, 2006). A reason for this correlation may be that in valvate aestivation the margins of two adjacent sepals are contiguous in a mirror symmetrical fashion and do not change position relative to each other during development. Thus, the space for the complicated petal to develop does not change its shape, and the petal lobes are unobstructed in their development. Such pinnate petals are also known from floral fossils (Carpenter & Buchanan, 1993). In these fossils, sepal aestivation is unknown, but it can be predicted that it was probably valvate not only because they appear to belong to Cunoniaceae, which often have valvate sepals (also in cases with simple or no petals), but also because of the presence of pinnate petals. Flowers with such lobed or pinnate petals in combination with a valvate calyx are known from many core eudicot families, especially in rosids (some Myrtaceae, Onagraceae, Rhynchocalycaceae, Anisophylleaceae, Cunoniaceae, Elaeocarpaceae, Celastraceae, Rhizophoraceae; Matthews et al., 2001; Matthews & Endress, 2002, 2004; Schönenberger & Conti, 2003; Endress & Matthews, 2006).

Conclusions

The mechanisms of the imprinting of organ shapes by contiguous neighboring organs are unexplored. From the diversity of cases, it appears that there are different degrees of imprinted shapes. There are directly imprinted shapes (such as in the stamens of *Sphenostemon*), and shapes that just fit in the general architecture and may not be directly shaped during the individual development but were installed during evolution (such as in the floral primordia of *Euptelea*). The stamens of Annonaceae may exhibit different levels of imprinting. A more general level may form the cuneate shape, and a more individual level may form the individual deformations that are different in each single stamen. It may not always be easy to recognize to what extent one or the other is involved.

The observations discussed in this paper should entice further and more detailed studies of interrelationships between the whole and the parts of structural systems in plants. I hope they will also help in the reconstruction of fragmentary fossil material. There are certainly more influences of the whole architecture on the shape of single parts than those shown here, which represent conspicuous examples.

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Appendix 1. List of plant specimens, collectors, and collection numbers used for original illustrations. Collection dates are provided in cases without a collection number. All vouchers deposited in Z.

Acsmithia davidsonii (F. Muell.) Hoogland, Cunoniaceae, *A. K. Irvine 1212*

Artabotrys hexapetalus (L. f.) Bhandari, Annonaceae, *P. K. Endress 5288*

Barringtonia calyptrata R. Br. ex Benth., Lecythidaceae, *P. K. Endress 4306*

Cananga odorata Hook. f. & Thomson, Annonaceae, *P. K. Endress 1134*

Carpinus betulus L., Betulaceae, *P. K. Endress 923* (Figs. 11, 15G, H), *3794* (Fig. 13D–F), *3795* (Figs. 12A–H, 13A–C), s.n., 7 IV 1968 (Fig. 15H)

Casearia silvana Schltr., Salicaceae, *P. K. Endress 6019*

Couroupita guianensis Aubl., Lecythidaceae, *P. K. Endress 9393*

Cyathocalyx martabanicus Hook. f. & Thomson, Annonaceae, *P. K. Endress 9372*

Euptelea polyandra Siebold & Zucc., Eupteleaceae, *P. K. Endress s.n.*, summer 1968

Fothergilla major Lodd., Hamamelidaceae, *P. K. Endress 717*

Geissois biagiana F. Muell., Cunoniaceae, *P. K. Endress 9211*

Gillbeea adenopetala F. Muell., Cunoniaceae, *P. K. Endress 4273*

Hamamelis virginiana L., Hamamelidaceae, *P. K. Endress s.n.*, 23 IX 1988

Heisteria parvifolia Sm., Olacaceae, *P. K. Endress 97-11*

Hydrocharis morsus-ranae L., Hydrocharitaceae, *K. Urmi König s.n.*, s.d.

Mayaca sp. indet., Mayacaceae, *P. K. Endress 9504*

Mimosa spegazzinii Pirotta, Leguminosae, *P. K. Endress 9723*

Munroidendron racemosum (C. N. Forbes) Sherff, Araliaceae, *P. K. Endress 96-10*

Piper augustum Rudge, Piperaceae, *P. K. Endress 7890*

Pistia stratiotes L., Araceae, *P. K. Endress 4688*

Platanus orientalis L., Platanaceae, *P. K. Endress 2032*

Polygonum filiforme Thunb., Polygonaceae, *P. K. Endress 5261*

Sphenostemon lobosporus (F. Muell.) L. S. Sm., Sphenostemonaceae, *P. K. Endress 9265*

Thunbergia alata Sims, Acanthaceae, *P. K. Endress 7871*

Thunbergia grandiflora Roxb., Acanthaceae, no voucher (photo of flower in Z)

Trichocladus grandiflorus Oliv., Hamamelidaceae, *W. Rauh & Schlieben 9737*

Wilkiea sp. indet., Monimiaceae, *B. P. M. Hyland 10127*